Quick guide

Velvet worms

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What is a velvet worm? Velvet worms are terrestrial, soft-bodied, many-legged carnivores. They form the phylum Onychophora ('claw bearers' — each of their many limbs terminates in paired claws). Velvet worms range in size from around 10 millimetres long to relative giants in excess of 20 centimetres, and known species have between 13 and 43 pairs of stubby limbs termed lobopods. Unlike arthropods, velvet worms do not have an exoskeleton, hence their limbs have no need for joints to facilitate mobility. On the head is a pair of sensory antennae, and small eyes. The mouth has a characteristic set of sclerotised jaws, and is flanked by two prominent papillae — the source of the animals' unique mode of prey capture discussed below. The skin is velvety because of the presence of dermal papillae covered with hydrophobic scales. Velvet worms come in many colours among and even within species, possibly a camouflage function (Figure 1). They have a certain mystique given their 'ancient' appearance and various curiosities, and a popular appeal — velvet worms are among few invertebrates for which dedicated conservation reserves have been created (in Australia, New Zealand and Brazil).

Where do they live? Restricted by a total lack of the ability to retain water (in physiological experiments, they act like a wet sponge), velvet worms typically inhabit temperate and tropical moist forests, where they live in rotting wood, leaf litter or soil, and more rarely, other moist environments such as caves. The ~180 species of living Onychophora currently named are divided into two families with distinct geographical distributions and biology, the Peripatidae and Peripatopsidae. Peripatidae are found in the tropics and sub-tropics of South-East Asia, the Caribbean, South and Central America and West Africa. Peripatopsidae are found in Chile, South Africa, Australia, New Guinea and New Zealand, a distribution suggesting that the origin of this family goes back to before the Gondwanan supercontinent broke up, and thus that they were already diverged from the Peripatidae. Over half of named species have been described very recently, and it is likely that many, many more await discovery. For example, genetic and morphological studies in Australasia, South Africa and Latin America are indicating that there may be one to two orders of magnitude more species than thought less than three decades ago.

Figure 1. A gallery of velvet worms.
A selection of velvet worm species from Australia. Original photographs by Jenny Norman, Noel Tait and Paul Sunnucks.

They move very slowly: so how do they catch their prey? Ambling along on their stubby legs, velvet worms are ambush predators. They emerge at night to hunt, and slowly patrol their environment seeking food — usually arthropods. Their sensitive antennae and skin can detect the touch of their quarry, such as an arthropod leg or feeler. After a brief period of investigation, the velvet worm may choose to rear up its head and, in a fraction of a second, launch its unique weapon: a stream of quick-setting, slimy glue. The slime papillae on either side of the head just under the antennae bear the openings of two large glands, and, like fire-hose nozzles, can be directed to point at the prey. The glands produce a solution of sticky proteins that is squirted out under high pressure. The jets of glue stick to everything they touch (except velvet worm skin), and the prey is quickly immobilised — struggling merely serves to further entrap the hapless prey. The velvet worm then approaches its subdued victim, and uses its sickle-shaped jaws, strong digestive enzymes and a sucking pharynx to consume its meal, often reclaiming its glue. The glue is interesting because it comprises natively disordered proteins, rather than highly-structured ones as found in spider silks, which form a gel that sets on drying into strong threads. These highly unusual substances contain components not known in any other animal, and their unique structure and properties may offer promise for biomaterials and biomedical applications.

How do they breed? With the exception of one known parthenogenetic species, velvet worms are sexually reproducing. However, they are remarkably diverse in the way they produce young. Some are fully live-bearing (viviparous), with well-developed placenta-like, extra-embryonic structures that attach to the mother's uterine wall and nourishes growing embryos until the birth of sequences of self-reliant, mini velvet worms. Other species are ovoviviparous, with the young hatching shortly before emergence from a mother's genital opening. In the true egg-laying (oviparous) species, beautifully sculpted shells protect eggs in the soil upwards of a year before hatching.

While mating has been observed in only a very few species, it is clear that modes of copulation are also diverse. Some species show dermal-haemocoelic (body cavity) insemination, in which sperm deposited in proteinaceous packages (spermatophores) on the skin of females make their way into the haemocoel through a lesion in the body wall across the haemolymph, to the ovary. Other species mate in a more common fashion, with delivery of spermatophores via direct contact between male and female genitalia. Copulation is truly bizarre in some Australian species in which spermatophores are transferred to the female by species-specific, ornate structures on the heads of males. The sole published study to date of genetic paternity indicates complex patterns of fatherhood among embryos within and between the two uteri in a female. Given complex female reproductive anatomy, such as long-term sperm-stores (spermathecae) and mysterious accessory pouches and ciliated funnels associated with them, there are major questions about female control of paternity and sperm competition. Development of young typically takes up to a year, but for most species, seasonality, mating and reproductive ecology remain mysterious.

At least some non-oviparous species care for their young, and there is strong evidence of sociality. The most studied species to date, *Euperipatoides rowelli* from Australia, shows unexpectedly sophisticated social behaviour, with dominance hierarchies built on a repertoire of signals, and 'consensual' sharing of resources.

What are they related to? Velvet worms have long been the subject of evolutionary speculation, which continues to the present day. One finding remains uncontroversial: Onychophora are grouped with the Tardigrada ('water bears', a phylum of microscopic, eight-legged, marine, freshwater and terrestrial animals) and Arthropoda in the superphylum Panarthropoda, based on a number of considerations including the presence of legs, segmentation, moulting and the organisation of the central nervous system. Understanding of the relationship of Panarthropoda to other animals has changed radically in recent years. The segmented, lobopod-limbed velvet worms share several features with the annelid worms, and thus the Panarthropoda were supposed to form a major group with Annelida: the 'Articulata'. This hypothesis is now thought to be mistaken.

Molecular phylogenetic evidence robustly places the Panarthropoda in a group of moulting animals, the Ecdysozoa, that also includes the legless, unsegmented Nematoda and a number of other minor phyla. The Annelida are now placed in a sister group to Ecdysozoa, the Lophotrochozoa, along with Mollusca, Brachiopoda and others. This phylogeny implies that segmentation and limb-like structures have evolved independently at least twice in the non-vertebrates, unless one proposes that the many legless and unsegmented phyla in Ecdysozoa and Lophotrochozoa have each independently lost their limbs and segments.

Fossil Onychophora are rare, but have been described from amber deposits (~30 to 40 million years old) and in chert nodules (~300 million years old). Unfortunately, owing to their rarity, geographic distribution and poor preservation of informative characters, these fossils are not very informative as to onychophoran relationships. Strangely, they have been found mostly in the temperate northern hemisphere, even though extant species occur predominantly in the southern hemisphere and are unknown north of 28 degrees. Going much further back in time, many armoured lobopod animals have been described from marine deposits from the base of the Cambrian to the Ordovician (~540 to 440 million years ago) and it is thought that these represent distant relatives of today's strictly terrestrial Onychophora.

What can they tell us about arthropod evolution? The arthropods are a pre-eminently successful phylum, with millions of extant species playing key roles in the biosphere. Understanding the origins and development of the basic body plan of arthropods is thus of great importance. Centuries of investigation and speculation have not yet resolved the internal structure of Arthropoda, so the evolutionary relationships of the major classes and many physical features are still under debate. To polarise arthropod trees, and define the likely morphological characters and developmental mechanisms of the arthropod ancestor, analysis of sister phyla in the Panarthropoda is required. Tardigrada are all very small, likely to have highly modified developmental processes, and have highly idiosyncratic morphology, and so may be of limited use in this regard. Onychophora have provided fertile ground for investigation.

Examination of velvet worm body patterning has shown that the animals have a mix of segmental and non-segmental features. Externally, the obvious segmental arrangement of the limbs is matched by some other structures (such as excretory organs) but not by others (for example, there are no obvious segmental borders in the body wall). Some segmentation genes first identified in insects are implicated in velvet worm segmentation (as they are in annelids), but overall their development is strikingly different from that of arthropods. For example, the arthropod (and tardigrade) post-cephalic nervous system is characterised by paired ventral nerve cords linked by segmental ganglia; in Onychophora, evidence for segmental ganglia is absent — there are paired ventral cords, but no segmental patterning other than that imposed by the presence of the serially repeated legs. The tripartite arthropod brain was thought to have a counterpart in Onychophora, but recent cell-level and developmental analyses have shown that, while the proto- and deuterocerebral regions have neural input from antennae and jaws, no putative third part innervating the slime papillae could be identified. The tritocerebrum thus seems to be an arthropod innovation.

What resources are available for velvet worms? While zoological and developmental studies of velvet worms have a long history, they are challenging to develop into fully-fledged ‘model organisms’. They are difficult to keep in captivity, have rarely been bred, have long reproductive cycles, and there are few legal and ethical routes to obtaining live specimens: they are typically highly endemic but live at low population densities. As velvet worms are mostly internal brooders, obtaining early-stage embryos requires sacrifice of the mothers. Thus, most experimental publications involve specimens transported from the wild into the laboratory, alongside rewarding velvet worm field ecology. Consequently, there is no stock centre where one can get strains, no bank of mutants, and, surprisingly, so far, very little genomic or transcriptomic data (GenBank/EMBL only holds ~13,000 records for all Onychophora, and four complete mitochondrial genomes, compared to ~9 million records for arthropods, including 430 mitochondrial and nuclear genomes). While velvet worm expressed sequence tag projects have been used to identify genes for phylogenetic and functional analyses, onychophoran genomes have been estimated to be in the multi-gigabase range (from 1.5 to 2 times that of the human genome) and so full genome sequencing remains a substantial task.

Despite these challenges, because of their key position in the tree of animals and their fascinating biology, in recent years velvet worms have been the focus of some directed molecular and developmental research projects. The increasing ease of data generation and the delightful biology of these ‘living fossils’ should mean that these are but the first trickles of a flood of new data that will address key questions in understanding the animal diversity and function of our planet.

Where can I find out more?

Encyclopaedia of Life *Onychophora* http://www.eol.org/pages/6927
Georg Mayer’s *Onychophora website* http://www.onychophora.com/ hosts an almost complete bibliography of velvet worm literature
Haritos, V.S., Niranjane, A., Weisman, S., Trueman, H.E., Sriskantha, A., and Sutherland, T.D. (2010). Harnessing disorder: onychophorans use highly unstructured proteins, not silks, for prey capture. Proc. R. Soc. Lond. B *277*, 3255–3263.
Mayer, G., Whitington, P.M., Sunnucks, P., and Pflüger, H.J. (2010). A revision of brain composition in Onychophora (velvet worms) suggests that the tritocerebrum evolved in arthropods. BMC Evol. Biol. *10*, 255, http://www.biomedcentral.com/1471-2148/10/255.
Reinhard, J., and Rowell, D.M. (2005). Social behaviour in an Australian velvet worm, *Euperipatoides rowelli* (Onychophora: Peripatopsidae). J. Zool. *267*, 1–7.
The University of California Museum of Paleontology, Berkeley *Onychophora and the fossil record* http://www.ucmp.berkeley.edu/onychoph/onychophora.html

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Q & A

Tony Hyman

Tony Hyman was born in Haifa Israel, and moved to London as a young boy. He stayed in London for his undergraduate work at UCL and then did his PhD in Cambridge at the Laboratory of Molecular Biology (LMB). After postdoctoral work at UCSF with Tim Mitchison, he moved to a group leader position at EMBL before becoming a founding director of the Max Planck Institute of Cell Biology and Genetics in Dresden. He was awarded the EMBO gold medal in 2003 and elected a Fellow of the Royal Society in 2007 and this year won the Leibnitz prize from the German Research Foundation, DFG.

What turned you on to biology in the first place? I can’t say that I ever had a flash of inspiration that I should become a biologist. I was a dreamy child who used to sit in the middle of the classroom, got middle-of-the-road marks and drifted through my school career. I grew up in London and went to St Marylebone grammar school, subsequently closed by the drive to change London schools from a selective to a comprehensive system. As with so many of those grammar schools, St Marylebone had first class committed teachers and a science block full of labs. We were doing physics, chemistry and biology soon after we started; so in a sense I was fully inculcated with science from an early age. Three A levels in science left one very well trained.

What was your first lab experience? After I left school I was not sure what to do, and worked as a lab technician at the UCL department of Zoology. My job was to make up the tissue culture media. At that time, I had to make the filters by putting a 0.2 micron filter in a metal case and autoclaving it. This was the old school way. Then I discovered that you could also get disposable filters, and that some of the younger professors had these. So I started getting in really early in order to use these filters. I knew that, if they found out I was not using the metal holders, I would be in trouble! One morning at about six, I found Terry Preston in his lab, and it turned out he had been there